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A NEW INFRAGENERIC CLASSIFICATION OF *HEVEA*

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I. HISTORICAL CONSIDERATIONS ON INFRAGENERIC CLASSIFICATIONS

The genus *Hevea*, now the source of 98% of the world's natural rubber, was first known to botany in 1775, when Aublet accurately and thoroughly described *Hevea guianensis* from French Guiana. For half a century, this was the only species known to science.

In 1824, Willdenow recognized a rubber-yielding tree collected near the mouth of the Amazon as a distinct species and, without actually describing it, he named it *Siphonia brasiliensis*. A year later, Humboldt, Bonpland and Kunth described as *Siphonia brasiliensis* a plant from the Orinoco, where what we know as *Hevea brasiliensis* does not occur. Since Willdenow's species is what we now recognize as true *H. brasiliensis* and since, in lieu of a description, he published diagnostic drawings of the critical parts of the plant, his "description" of *H. brasiliensis* is accepted on the basis of priority.

The genus *Siphonia* was later shown to be congeneric with *Hevea*. *Siphonia brasiliensis* was transferred by Mueller Argoviensis in 1865 to *H. brasiliensis*.

In 1854, five new species were described (under *Siphonia*) by Bentham, and the following year another was proposed by Spruce — all on the basis of the extensive collections sent from Brazil by the English plant explorer, Richard Spruce.

By this time, Bentham believed that some kind of infrageneric classification could be significant in understanding the genus. He put what he then called *Siphonia elastica*, *S. brasiliensis*, *S. discolor*, *S. Spruceana* and *S. pauciflora* into one Section, characterized by a sessile, divaricate-trilobed stigma; into another section, he placed *S. lutea* and *S. rigidifolia*, with a short, attenuate style. It is now recognized that this classification groups together species that are not closely related. Bentham pointed out, however, that, prior to Spruce's field studies, little was known about floral structure in the genus: he wrote that, although the characters "have been verified in each instance in several, and often, in many flowers . . . it remains to be seen how far they may prove constant when we have specimens from a greater variety of sources".

A second attempt to an infrageneric classification was made in 1858 by Baillon in his *Etude générale du groupe des Euphorbiacées*. Using the epithet *Siphonia*, Baillon divided the species then known into two Sections: *Hevea* and *Bisiphonia*. Pointing out that there were, among the concepts then recognized, species which were intermediate, he placed what are now called *Hevea guianensis* and its variety *lutea* in Section *Hevea*; what are now known as *H. brasiliensis*, *H. pauciflora*, *H. Spruceana*, *H. Benthamiana* and *H. rigidifolia* he included in *Bisiphonia*. The former Section had an isostemonous androecium and no disk, or, at best, an inconspicuous one; the latter, was characterized by having a diplostemonous androecium and a more or less well developed disk. Later, in 1864, Baillon merely enumerated seven species (unexplainably omitting *H. guianensis*) without making mention of an infrageneric classification.

Baillon's infrageneric classification of *Hevea* into two groups, sections or series has come down to the present time, even though in recent years its naturalness has been questioned and its acceptance has been denied by most taxonomists who have worked on the genus during the past thirty years.

In 1865, Mueller offered his classification of the Euphorbiaceae, placing the genus *Hevea* in Subtribe *Heveae* — the only genus in this subtribe. He divided *Hevea* into two Sections: *Euhevea* (equivalent to Baillon's Section *Hevea*), made

up of one species, *H. guianensis*; and Section *Bisiphonia* (the same as Baillon's Section *Bisiphonia*) comprising what are now known as *H. Benthamiana*, *H. brasiliensis*, *H. guianensis* var. *lutea*, *H. pauciflora*, *H. rigidifolia* and *H. Spruceana*. In 1866, he revised his family classification of the Euphorbiaceae but maintained his earlier infrageneric classification of *Hevea* with the same number of species. His only change in treatment consisted in a grouping together of the species of Section *Bisiphonia*, according to the shape of the staminate buds: *H. Spruceana* (with subovoid, obtuse buds with a calyx lacinate for only slightly more than half its length); *H. pauciflora* (with ovoid, obtuse buds, with a calyx divided for 2/3 and 3/4 its length); and *H. rigidifolia*, *H. Benthamiana*, *H. brasiliensis* and *H. guianensis* var. *lutea* (with oblong-conic-ovoid and acute buds, apically slightly twisted). Again, in 1874, Mueller divided the genus, as he had done previously, into *Euhevea* (*H. guianensis*) and *Bisiphonia* (all other species). At this time, he arranged the species in *Bisiphonia* into only two groups: those with staminate buds obtuse (*H. Spruceana*, *H. pauciflora*) and those with buds acuminate (*H. rigidifolia*, *H. nitida*, *H. Benthamiana*, *H. brasiliensis* and *H. guianensis* var. *lutea*).

No further attention was apparently given to infrageneric classification of *Hevea* until 1906, when Huber initiated his detailed studies of the genus. Huber, the first botanist acquainted with living trees in their native habitat to consider *Hevea* generically from a taxonomic viewpoint, followed the earlier division of *Hevea* into *Euhevea* and *Bisiphonia*. Under *Bisiphonia*, however, he made three Series, giving them technical Latin designations. Into Series *Luteae* he put what he recognized as *H. lutea*, *H. apiculata*, *H. cuneata*, *H. Benthamiana*, *H. Duckei*, *H. paludosa* and *H. rigidifolia*: with anthers in two incomplete whorls and staminate buds acuminate; these specific concepts he separated into three groups on characters in the disk of the staminate flower. Series *Intermediae* comprised his *H. minor*, *H. microphylla*, *H. Randiana* and *H. brasiliensis*: with anthers in two complete whorls and acuminate buds; these species he divided into two groups, based on characters in the style. His Series *Obtusiflorae* included what he recognized as *H. Spruceana*, *H. discolor*, *H.*

similis, *H. pauciflora*, *H. confusa*, *H. nitida*, *H. viridis*, *H. Kunthiana*; he arranged these series into two groups based on characters of the disk of the pistillate flower, with the last three (incompletely known species) in a grouping which he called *Incertae sedis*.

Huber maintained that Section *Euhevea* is "very natural and well characterized". While quite distinct from *Euhevea*, *Bisiphonia* is, he confessed, "not very homogeneous and does not have a rational subdivision" — for which reason he set up his three Series.

As late as 1913, Huber still continued to maintain these two Sections and the three Series in *Bisiphonia*, believing that, in general, this treatment represented natural trends. He did state of Series *Luteae*, nonetheless, that "species in the Linnean sense seem almost non-existent in this group. . . . With the present state of our understanding, all appear to be in movement and fluctuation, and we must be satisfied if we arrive at a rational grouping of small, provisional species."

In 1910, Pax used the division of *Hevea* into Sections *Euhevea* and *Bisiphonia*, separating the two solely on the basis of the number and placement of the anthers. Of the 17 species that he accepted, he grouped three in *Euhevea* (*H. guianensis*, *H. nigra*, *H. collina*) and 14 in *Bisiphonia* (*H. Benthamiana*, *H. Duckei*, *H. nitida*, *H. paludosa*, *H. brasiliensis*, *H. lutea*, *H. rigidifolia*, *H. spruceana*, *H. similis*, *H. discolor*, *H. minor*, *H. microphylla*, *H. pauciflora*, *H. membranacea*). He pointed out that the flowers of *Hevea* exhibit few sharp characteristics of use in separating species and that the fruits and seeds, which might provide good differentiating characters, were not known for some species. He further pointed out that the differentiating character employed for Section *Bisiphonia* were not sharp, noting that he could find intermediates in the anthers of *H. guianensis* and *H. lutea*.

It is now clear that Pax's infrageneric classification, as well as those attempts that preceded his, were far from natural. Pax, a specialist in the Euphorbiaceae, was at a great disadvantage in not having seen *Hevea* growing in the natural state.

In 1929, Ducke wrote that "the natural system of the *Hevea* is still to be made; the species are very difficult to group

because of their affinities that are too close". It was not, however, until 1923 that he considered definitely the infrageneric divisions of *Hevea*: "While still awaiting fuller material of certain species, I have already been able to affirm that the sections *Euhevea* and *Bisiphonia* . . . are not so well defined as one has thought: I have found, amongst the many specimens of *H. guianensis*, some that have the anther-whorl slightly irregular due to the insertion of one of the anthers a little too low. In this same species, in trees of one single locality, the staminate buds vary from wholly obtuse (almost globose) to rather distinctly acuminate". This point of view he reiterated in 1935. Ducke's silence on this matter in later publications may be taken as an indication of abandonment of the whole system of grouping the species into subgeneric affinities. I know this to be true, for when we discussed this point in depth, he stated that he had no further use for the proposed infrageneric classifications that had been published. And our refusal to recognize these classifications was crystallized when, in 1945, we jointly reduced *Hevea lutea* (up to that time a typical member of *Bisiphonia*) to varietal status under *H. guianensis* (the only species of *Euhevea*).

Ducke spent more than half a century studying wild *Hevea* in the Amazon, and he was, undoubtedly, the taxonomist most thoroughly acquainted with *Hevea* over most of its natural range. Ducke's taxonomic outlook in *Hevea* underwent three distinct periods. In his earlier years, still under the influence of his teacher, Huber, Ducke often described minor variants as species (*H. gracilis*, *H. Huberiana*, *H. humilior*, *H. marginata*). In what we may consider his intermediate stage, he reduced some of these "species" to varieties and forms and described a large number of additional infraspecific variants. Towards the end of his life, he recognized a limited number of species and fewer varieties and forms, reducing many of the concepts that he himself had previously described.

In his papers on *Hevea*, Baldwin failed to discuss infrageneric classification. That he did not consider the available treatments as natural, however, may be inferred from several of his statements. An example is the following opinion: ". . . . Ducke found a tree which he considered to be inter-

mediate between *H. guianensis* and *H. lutea*, and for this and comparable reasons he and Schultes have recently made *lutea* a variety of *H. guianensis*. . . . One might with almost as much reason render the genus unispecific". In another context, he wrote that, while he preferred to recognize "nine — or fewer — species. . . .", "in nature and in various localities entities so intergrade that if one wishes . . . he could . . . reduce the genus to one species and consider it in terms of trinomials with many forms appended".

Nor did Seibert discuss in great detail Mueller's two Sections *Euhevea* and *Bisiphonia*, except to state that he had "arrived at the conclusion that exact number of anthers is of little taxonomic significance within the limits of certain tendencies", pointing out that the number of anthers "may vary within the species and between flowers on the same tree."

Ever since 1945, when, jointly with Ducke, I reduced *Hevea lutea* to varietal rank under *H. guianensis*, I have considered the classical infragenetic grouping of species to be both unworkable and unnatural.

II. HISTORICAL NOTES ON *HEVEA MICROPHYLLA*

A natural classification of species into infrageneric groupings should rest, whenever possible, preferably on several different characters — for example: both floral and fruit characters — in which little or no integradation is discernable. Extensive field work on wild *Hevea* in the Amazon and examination of thousands of specimens in the major herbaria have convinced me that such differences exist and that they may be used as the basis of an infrageneric classification which, in my opinion, is natural, showing two rather widely divergent trends in evolutionary development of the genus.

In 1905, Ule, who had spent a long period studying *Hevea* in numerous areas of the Amazon, described a most interesting species: *Hevea microphylla*, which he had collected in fruit in 1902 on the Ilha Xibarú, slightly downstream from the mouth of the Rio Branco on the Rio Negro in Brazil. Later exploration has shown that this species is endemic to the Rio Negro, from the middle to the upper course of the river.

In 1910, Pax treated the species as comprising two varieties: var. *typica* and var. *major*, on the basis of differences in size of the leaflets.

Unfortunately, *Hevea microphylla*, which only with the greatest difficulty and misunderstanding could be confounded with any other species, was, until recently, confused with Hemsley's *H. minor*, now considered to be a synonym of *H. pauciflora* var. *coriacea*. In 1906, Huber suggested that *Hevea microphylla* might be synonymous with *H. minor*, pointing out several characters in which the two concepts, as described, seemed to agree. He admitted, nonetheless, that there appeared to be differences in other characters, so he chose "to consider *H. microphylla* a distinct species for the present". Identifying erroneously a flowering collection of *H. microphylla* made by Ducke (*Ducke 7027*) in the lower-middle Rio Negro as *H. minor*, Huber published an extended description of *H. minor*. In describing the flowers of the Ducke specimens, Huber indicated still that the two species appeared to be close allies, although he believed that flowers were still unknown for *H. microphylla*. In 1913, he yet maintained *H. minor* and *H. microphylla* as distinct, including both in his Series *Intermediae* — as he had done previously — but intimating that further studies might make it necessary to remove *H. microphylla* and *H. minor* from Series *Intermedia* and, together with *H. rigidifolia*, to form a new Series for them.

Ducke apparently accepted Huber's identification of his flowering collection (*Ducke 7027*) as *Hevea minor*. He had collected topotypical material of *H. microphylla* (*Ducke HJBR23750*) which agreed in all characters with his earlier collection (*Ducke 7027*). Consequently, he reduced *H. microphylla* to synonymy under *H. minor* in 1935, maintaining this position in 1946.

In 1947, Baldwin indicated apparent acceptance of Ducke's treatment of *Hevea microphylla*.

In the same year, I studied the type material of *Hevea minor* collected on the upper Rio Negro near the confluence with the Casiquiare and herbarium specimens of the Ule and the Ducke collections of *H. microphylla*. It became apparent immediately that the two concepts were completely distinct and not in any

way closely allied. I published the results of my studies, indicating that *H. microphylla* is, indeed, the most unique species in the genus and that, in addition to morphological characters easily to separate it from all other species, there are, likewise, strong ecological differences setting *H. microphylla* apart from *H. minor*: periodically and deeply flooded forested river banks in the former; scrub-forest in sandy, almost permanently flooded caatingas in the latter. Seibert accepted my treatment of *H. microphylla* as distinct; and, in 1949, Ducke (in litt.) likewise followed my interpretation, although, in publishing his acceptance of it in 1950, he stated that it was "lamentable, because it would have been better, for true scientific purpose, if that change could have been avoided."

For several years following my article in 1947, I was able to carry out intensive plant exploration in the Rio Negro basin of Brazil, Colombia and Venezuela, studying abundant stands of *Hevea microphylla*. These studies substantiated the uniqueness of this species and led, in 1952, to a paper on its range and variability and an extended description of the concept. At that time, I wrote: There are so many differentiating characters of the first magnitude to be found exclusively in *H. microphylla* that we are forced to regard the concept as standing entirely alone with no close allies in the genus". In 1967, whilst on the Alpha-Helix Amazon Expedition, I was fortunate again to meet with extensive stands of *H. microphylla*, not too distant from the type locality. These studies intensified my belief that we were concerned here with a species that had gone off on an evolutionary tangent of its own and that it, therefore, merited some special recognition in any treatment of infrageneric classifications of the genus.

III. THE UNIQUENESS OF *HEVEA MICROPHYLLA*

Hevea microphylla stands quite alone in the genus. It is unique in several basic characters — characters in both the flower and fruit and which are so distinct that there appear to be no intermediates.

The pistillate flowers of *Hevea microphylla* differ markedly from those of all other species in having a greatly swollen torus

which is conspicuous not in the flowers but also at the base of the fruit. A torus is present, of course, in the pistillate flowers of all species but, except for *Hevea pauciflora*, it is so inconspicuous as to be for all practical purposes of taxonomic use essentially non-existent. In *H. pauciflora*, it is sufficiently pronounced as to be easily visible, but it in no way approaches the size and conspicuousness of that of *H. microphylla*, nor is it obvious at the base of the ripened fruit.

The fruit is unique in being pyramidal, triangular in cross section, conspicuously keeled and with a long-acute apex. The carpel walls are thin and leathery, made up of a thick-papery pericarp and an excessively thin, coriaceous endocarp. In all other species, the capsule is subglobose, ovoid or ellipsoid, trigastic or round in cross section, and emarginate, with a rounded or slightly mucronate tip. The carpel walls are thick and ligneous, made up of a more or less fleshy pericarp and a heavy, thick, woody endocarp.

This unique structure of the capsule of *Hevea microphylla* is strongly reflected in the method of seed dissemination. In *H. microphylla*, the capsule dehisces slowly, not explosively, and the valves open gradually, twisting as they dry out, and adhere to the receptacle long after dehiscence. The seeds gently drop directly from the capsule and are not propelled violently a great distance from the tree. In all other species, the capsule opens explosively, usually sending the seeds in several directions far beyond the area beneath the crown of the tree. The heavy, ligneous valves contort only slightly, if at all, and fall to the ground at the moment the capsule bursts open and frees the seeds. Only in *Hevea Spruceana* are the heavily ligneous valves persistent and, although the capsule does open explosively, the seeds are not propelled so far as in other species, primarily because of their greater size and weight.

IV. INFRAGENERIC CLASSIFICATION

Hevea Aublet, Hist. Pl. Guian. Franç. 2 (1775) 871.

Subgenus **Hevea**

Typus: *Hevea guianensis* Aublet

Flos pistillatus toro valde inconspicuo, capsula matura haud

manifesto. Capsula subglobosa, ovoidea vel ellipsoidea (nunquam pyramidalis), transversaliter trigistra vel circularis, ecarinata, apice rotundata vel parum mucronata, eruptione dehiscens, semina ab arbore distante propullulans. Valvae crassae, pericarpio plus minusve carnosio atque epicarpio grosso, denso, lignoso, siccitate non convolutae, usualiter non perdurantes.

The following species and varieties, as the genus is now understood, belong to this subgenus.

Hevea Benthaminana Mueller Argoviensis in *Linnaea* 34 (1865) 204.

Hevea brasiliensis (Willd. ex A. Juss.) Mueller Argoviensis loc. cit. 204.

Hevea camporum Ducke in *Arch. Jard. Bot. Rio Jan.* 4 (1925) 111.

Hevea guianensis Aublet loc. cit. 871.

Hevea guianensis Aublet *var. lutea* (Spr. ex Benth.) Ducke et R.E. Schultes in *Caldasia* 3 (1945) 249.

Hevea guianensis Aublet *var. marginata* (Ducke) Ducke loc. cit. 6 (1933) 51.

Hevea nitida Martius ex Mueller Argoviensis in *Martius Fl. Bras.* 11, pt. 2 (1874) 301.

Hevea nitida Martius ex Mueller Argoviensis *var. toxicodendroides* R.E. Schultes et Vinton) R.E. Schultes in *Bot. Mus. Leafl., Harvard Univ.* 13 (1947) 11.

Hevea pauciflora (Spr. ex Benth.) Mueller Argoviensis in *Linnaea* 34 (1865) 203.

Hevea pauciflora (Spr. ex Benth.) Mueller Argoviensis *var. coriacea* (Ducke) Ducke in *Arch. Inst. Biol. Veg. Rio Jan.* 2 (1935) 239.

Hevea rigidifolia (Spr. ex Benth.) Mueller Argoviensis loc. cit. 203.

Hevea Spruceana (Benth.) Mueller Argoviensis loc. cit. 204.

Subgenus **Microphyllae** R. E. Schultes *subgen. nov.*

Typus: *Hevea microphylla* Ule

Flos pistillatus toro manifeste incrassato capsulae maturae ad basim persistente, conspicuoque. Capsula pyramidalis, transversaliter triangularis, conspicue carinata, apice longe

acuta, lente paulatimque (non eruptione) dehiscens, semina directe sub arbore cadens. Valvae tenues, coriaceae, pericarpio crassipapyraceo atque endocarpio tenuissimo chartaceoque, siccitate valde convolutae, perdurantes.

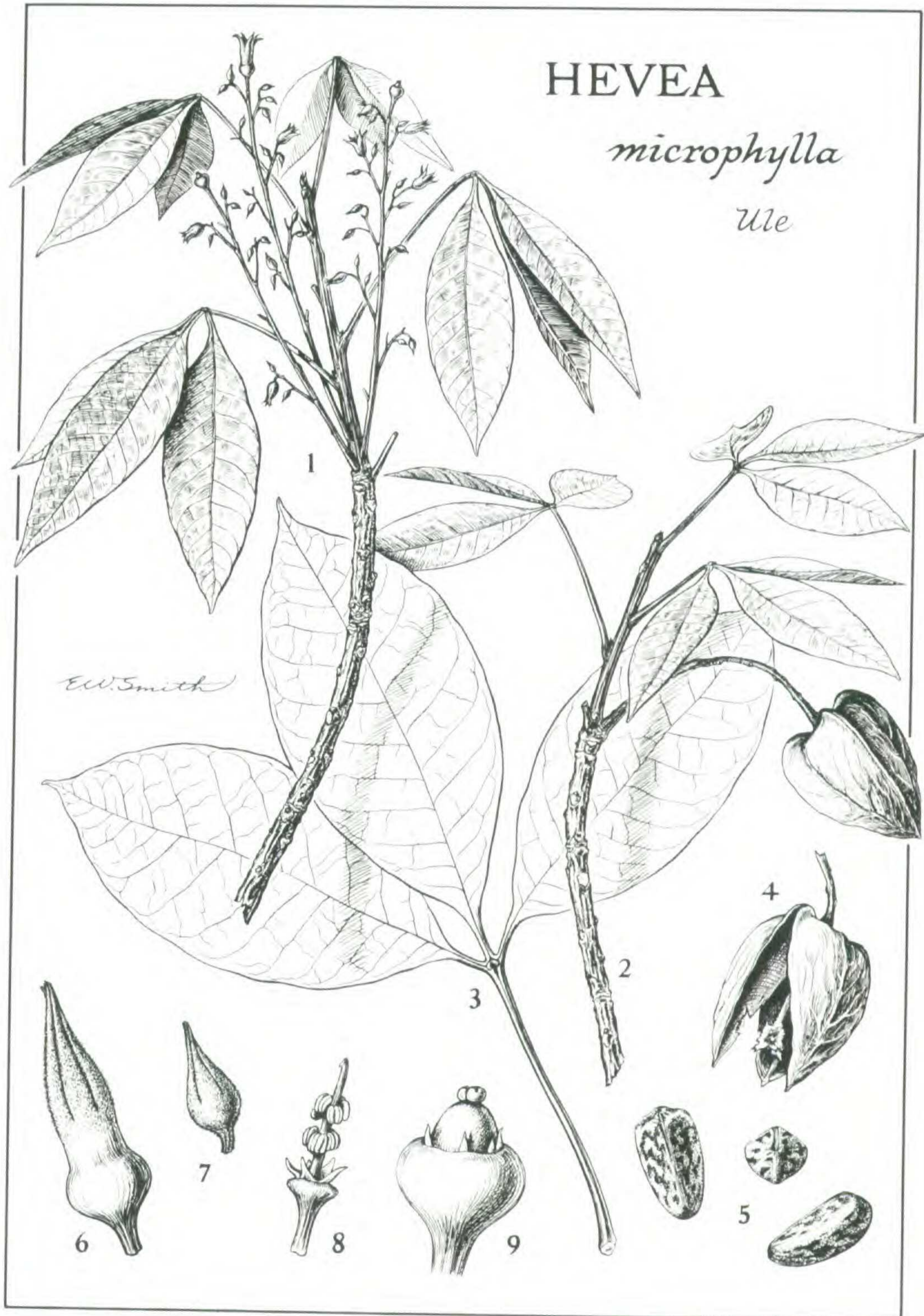
The only species in this subgenus is

Hevea microphylla Ule in Engler Bot. Jahrb. 35 (1905) 669.

EXPLANATION OF PLATE 51

1 and 2, habit. 3, leaf showing departure from normal shape. 4, valves of capsule showing mode of dehiscence. 5, seed. 6, pistillate bud, showing terminal spiralling. 7, staminate bud. 8, staminate flower with calyx removed. 9, pistillate flower with calyx removed, showing large torus.

Drawn by ELMER W. SMITH



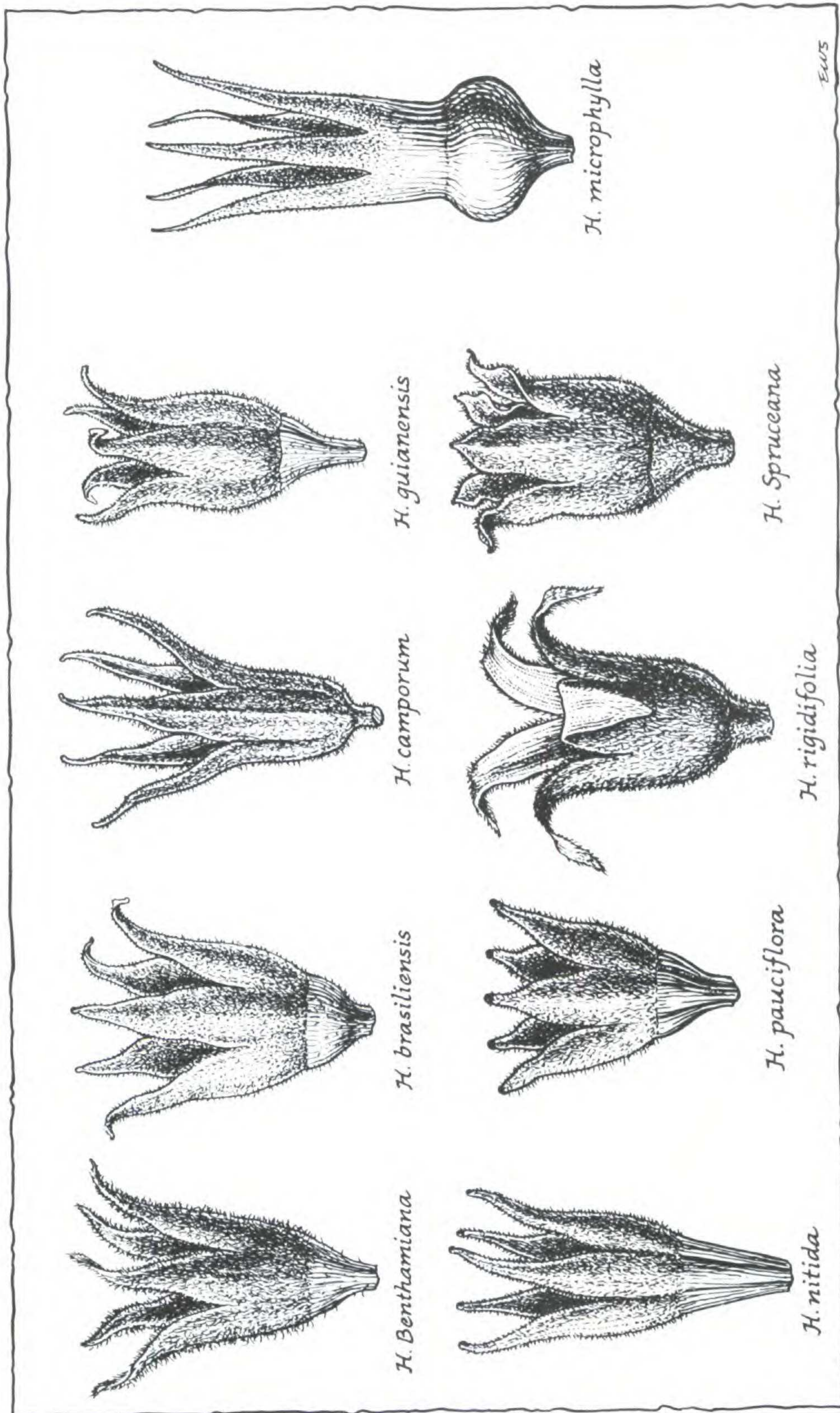


Plate 52. Comparison of the pistillate flowers of the nine known species of *Hevea*. Drawn by E. W. Smith.

